Systematic studies in subfamily Celastroideae (Celastraceae) in southern Africa: reinstatement of the genus *Gymnosporia*

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Gymnosporia (Wight & Arn.) Hook. f., *nom. conserv.*, is recognised as a genus on its own, comprising all the spiny members currently included in the genus *Maytenus* Molina *s.l.* Diagnostic characters of *Gymnoporia* include the presence of brachyblasts and spines, leaves in fascicles on older branches or alternate on young ones, inflorescence a monochasium, subdichasium or dichasium, and flowers mostly unisexual. *Gymnosporia* is an Old World genus comprising about 80 species and subspecies, occurring in most of Africa, Madagascar and adjacent islands, southern Spain, the near Middle East, Pakistan, India, Sri Lanka, extending to the Far East, Malesia, Papua New Guinea, the Philippines, Taiwan, Queensland (Australia) and the Polynesian Islands. An amplified generic description is provided. Differences and similarities between the spiny genera of Celastroideae [*Putterlickia* Endl., *Gloveria* M.Jordaan, *Gymnosporia* (Wight & Arn.) Hook. f. and *Moya* Griseb.] are tabulated.

Keywords: Celastraceae, *Gloveria*, *Gymnosporia*, *Maytenus*, *Moya*, *Putterlickia*, southern Africa, taxonomy.

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Introduction

The Celastraceae (including Hippocrateaceae) is a family of trees, shrubs or climbers, comprising about 85 genera (Brummitt 1992). The family is widespread, but concentrated in subtropical and tropical regions. Subfamily Celastroideae (Loesener 1892, 1942; Scholz 1964; Takhtajan 1980), a natural assemblage of taxa, is characterised by dry loculicidally dehiscent capsules and seeds with an aril. In recent years the African, Madagascan, Asiatic and Australian members of subfamily Celastroideae (Celastraceae) have been classified under *Catha* Forssk. ex Scop., *Celastrus* L., *Denhamia* Meisn., *Maytenus* Molina, *Moya* Griseb., *Polycardia* Juss., *Pterocelastrus* Meisn. and *Putterlickia* Endl. Many genera have a limited distribution range, e.g. *Celastrus* occurs in Eurasia, Madagascar, Malesia, Australia and North America but is absent from the African continent; *Denhamia* is confined to Australia; *Polycardia* to Madagascar; *Moya* to South America; *Pterocelastrus* and *Putterlickia* to southern Africa and *Catha* to Africa and SW Arabia. *Maytenus s.l.*, consisting of non-spiny and spiny shrubs or trees, is currently considered to be the most widespread genus in the subfamily, occurring in both the Old and New World. The purpose of the present paper is to review the development of generic concepts in the Celastroideae briefly and to present arguments for the reinstatement of the genus *Gymnosporia*.

Historical review

Members of the Old and New World genus *Maytenus* and Old World genera *Gymnosporia* and *Putterlickia* are all placed in *Celastrus* L. by most early authors, e.g. Linnaeus (1753, 1754), Miller (1768), Linnaeus filius (1781), Lamarck (1785), Thunberg (1794, 1823), Willdenow (1798), Burchell (1824), De Candolle (1825), Ecklon & Zeyher (1834–1835), Meyer (1843), Schlechtendal (1846), Sonder (1860), Oliver (1868), Kuntze (1891, 1898) and Wood (1908). Kunth (1825), however, pointed out that some *Celastrus* species have a combination of peculiar characters and that they may well constitute a new genus, although he did not formally propose a name for it.

Reporting on the Indian species of *Celastrus*, Wight and Arnott (1834) divided *Celastrus* into two sections, *Eucelastrus* and *Gymnosporia* (from the Greek *gymnos* = naked, and *spora* = seed), on the basis of ovary and seed characters. In section *Eucelastrus* the ovary is free from the disc and the seed completely enclosed by a fleshy aril. This section corresponds to the genus *Celastrus* as circumscribed today (Ding Hou 1955). It occurs in eastern Asia, Oceania, both Americas and Madagascar, between 40° S and 47° N. In section *Gymnosporia*, which corresponds to Kunth's (1825) unnamed genus, the ovary is half immersed in the disc, with the seed completely or incompletely enclosed by an aril.

Don (1832) delineated the order Celastrineae tribe Euonymeae as plants with arillate seeds and simple leaves and placed the spiny African, European and Asiatic members of *Celastrus* in the genus *Catha* Forssk., a genus with hermaphroditic flowers. He recognised *Celastrus* Kunth (1825) *non* L. (excluding *C. scandens* L.) as a genus with dioecious plants and ovaries which are 2–4-locular with two ovules per locule. Don (1832) also recognised *Maytenus* as an exclusively American genus, characterised by polygamous flowers, one ovule per locule and the lack of spines. Endlicher (1840, 1841) elaborated on Don's (1832) description of tribe Euonymeae, including all members with loculicidally dehiscent capsules. This resulted in the recognition of two more genera, namely *Pterocelastrus* Meisner (1837) for members with protuberances on the capsule and the newly described genus *Putterlickia* for species with more than two ovules per locule. Walpers (1842) maintained the genus *Putterlickia*, but still followed Don (1832) in placing the spiny Asiatic species of *Celastrus* under *Catha*. However, he returned Don's European and African members of *Catha* to *Celastrus* Kunth *non* L.

Hooker (1862) elevated section *Gymnosporia* Wight & Arn. to generic rank. This genus is geographically restricted to the Old World. The generic name *Gymnosporia* has subsequently been conserved against the following *nomina rejicienda* (Farr *et al.* 1979): *Catha* Forssk. ex Schreb. (1789); *Eucentrus* C. Presl (1844) ex Endl. (1850); *Polyacanthus* C. Presl (1844).

Distinguishing characters used by Hooker (1862) to separate *Gymnosporia* from *Maytenus* are as follows: 'locule with two ovules; plants often spiny; inflorescences cymose — *Gymnosporia*. Locule with 1 (rarely 2) ovules; plants without spines; flowers solitary, or inflorescences fasciculate or cymose — *Maytenus*'. He gave the geographical distribution of

Gymnosporia as Spain, Africa, Asia and Australia, and that of *Maytenus* as tropical America and Australia. These generic concepts were followed by subsequent workers such as Szyszylowicz (1888), Sim (1907), Loesener (1893, 1896), Engler and Gilg (1912), Schonland (1919), Marloth (1925), Davison (1927) and Adamson (1950).

In his monumental worldwide revision of the Celastraceae, Loesener (1892, 1942) was the first to establish subfamilies and tribes in the family. He referred all the Old World spiny members of Celastroideae with short and long shoots and fasciculate leaves to subfamily Celastroideae, tribe Eucelastreae. Loesener (1942) recognised *Gymnosporia* as an Old World genus, *Maytenus* as a genus occurring in both the Old and New World and *Celastrus* as being absent from Africa. Allowing for the limited knowledge on many genera that existed at that time, the classification proposed by Loesener (1942) is a suitable starting point for expressing the broad outlines of generic relationships within the family.

Exell and Mendonça (1952) and Exell (1953) argued that Loesener's (1942) separation of *Gymnosporia* from *Maytenus*, on the basis of the presence of either thorns or the inflorescence borne on short shoots in *Gymnosporia*, appeared artificial. They proposed an amalgamation of the two genera into a widely circumscribed *Maytenus s.l.* Brenan (1953) shared the latter view, and added that *Maytenus* had previously been segregated from *Gymnosporia* by what he considered rather vague characters, such as the prevalence of uniovulate locules and bilocular ovaries, whereas species with biovulate locules and with spines were placed in *Gymnosporia*.

Ding Hou (1955) examined a very large number of herbarium specimens of *Celastrus*, *Gymnosporia* and *Maytenus* and compared many characters. He concluded that these three genera were distinct, and proposed their recognition on the basis of a combination of several characters, not a single character on its own. Exell (1953), Blakelock (1954) and Marais (1960), however, claimed that there seemed to be no single character state, nor any combination of characters, constant enough to justify the retention of *Gymnosporia*. They also agreed that *Celastrus* was a good genus, and that it was absent from the African continent. *Celastrus* is characterised by a scandent habit, an ovary free from the disc, a persistent central axis of the capsule, and a frequently racemose or paniculate inflorescence.

Ding Hou (1962) changed his mind and stated that the differences between *Gymnosporia* and *Maytenus* as tabulated in his paper of 1955 cannot be maintained, especially not in the African flora, as was also concluded by Marais (1960). Ding Hou (1962) retained only *Celastrus* and *Maytenus*, distinguished by a combination of three characters: habit, degree of adnation of ovary and disc, and fruit structure.

The first major taxonomic treatment of spiny Celastroideae was by Thunberg in his *Flora capensis* (1823). Ecklon & Zeyher (1834–1835) were the first to note the extreme variability of Linnaeus's (1753) *C. buxifolius*. Don (1832) placed all the species under *Catha*; Presl (1844) described two new genera, namely *Eucentrus* and *Polyacanthus*, both now included in *Gymnosporia*, established by J.D. Hooker (1862). The second main revision was by Sonder (1860) in *Flora capensis*, a work in which all known spiny Celastroideae were treated under *Celastrus*. Szyszylowicz (1888) was the first to place all the species under *Gymnosporia* and *Putterlickia*, the latter described by Endlicher (1840). Loesener's publications on the Celastraceae (1892–1942) are very important as he attempted to include all known taxa in his monographs of the family. He was the first to transfer all biovulate spiny members to *Gymnosporia*.

The most recent comprehensive taxonomic revision of the Celastroideae for southern Africa, and in fact all the southern African Celastraceae, was by Davison (1927). In recent years the view that *Gymnosporia* is congeneric with *Maytenus* has been generally uncritically accepted and followed by botanists working on the African flora, for example Exell and Mendonça (1954) (Angola), Keay and Blakelock (1958) (Flora of West Tropical Africa region), Wilczek (1960) (Democratic Republic of the Congo, Rwanda and Burundi), Marais (1960) (Flora of southern Africa region), Ding Hou (1962) (Flora malesiana region), Robson (1966) (Flora zambesiaca region), Sousa (1968) (Guinea-Bissau), Robson and Sousa (1969) (Mozambique), Guillarmod (1971) (Lesotho), Ross (1972) (KwaZulu-Natal), Villiers (1975) (Cameroon), Compton (1976) (Swaziland), Troupin (1982) (Rwanda), Bond and Goldblatt (1984) (Cape Floristic Region), Jessup (1984) (Australia), Sebsebe (1985, 1989) (Sudan, Ethiopia, Eritrea, Djibouti, Somalia, Saudi Arabia, Yemen and Oman) and Robson (1994) (Uganda, Kenya and Tanzania).

Marais (1960) and Robson (1965, 1966), who were mainly followed in the two most recent lists of African plant species (Arnold & De Wet 1993; Lebrun & Stork 1992), had a very broad species concept. Only 12 spiny members of *Maytenus* are recognised in the Flora of southern Africa region (Arnold & De Wet 1993) and 30 in the Flora of tropical Africa, south of the Sahara (Lebrun & Stork 1992).

Reinstatement of *Gymnosporia*

A recent comparative study on the spiny (spines regarded as modified stems) members of the Celastroideae (Celastraceae) on a worldwide scale (Jordaan 1995; Jordaan in prep.) provided abundant evidence, both macroscopic and microscopic, for the segregation of *Maytenus s.l.* into two natural, more homogeneous genera. We consequently propose that *Gymnosporia* be reinstated as a genus, comprising all the spiny members currently placed in *Maytenus s.l.*, thus following the view of Loesener (1942) and Ding Hou (1955). *Maytenus* is provisionally retained in a 'strict sense' to accommodate all the nonspiny members. It remains, however, a heterogeneous assemblage, perhaps best further subdivided into a number of segregate genera. Morphological similarities and differences between the spiny genera of the Celastroideae are summarised in Table 1.

Maytenus s. str. differs from *Gymnosporia* in the absence of brachyblasts and spines, alternate leaves which are never in true fascicles, flowers always bisexual, and inflorescences which are solitary, fasciculate (reduced cymes), racemose (reduced panicles) or variously cymose (though apparently never dichasial cymes). Plants of *Maytenus s. str.* are mainly small to large forest trees, only a few species remaining low shrubs when growing near the coast or in arid regions, whereas only a few members of *Gymnosporia* are medium-sized trees, mostly not exceeding 10 m. In *Maytenus s. str.* the seeds are completely or almost completely enclosed by an aril, while different states occur in *Gymnosporia*: from completely enclosed to seeds with the aril reduced to a basal rim.

Gymnosporia has more characters in common with the spiny genus *Putterlickia* than with the members of nonspiny *Maytenus s. str.* Although *Gymnosporia* is morphologically diverse, it is easily recognised by a combination of five characters: (i) the presence of spines and brachyblasts; (ii) functionally unisexual flowers; (iii) a dichasial inflorescence type; (iv) bi-ovulate and (v) 2–4-locular ovaries. Plant material of *Gymnosporia* has been studied from all parts of its range and it is here reinstated as a distinct genus.

In habit, leaf, inflorescence and fruit characters *Gymnosporia* is very similar to *Putterlickia*, a mainly southern African genus (Table 1). These two genera are distinguished mainly on the basis of floral sexuality and the number of ovules per locule. *Putterlickia* has bisexual flowers and usually 6–12 ovules per

Table 1 Summary of selected morphological similarities and differences between the spiny genera of Celastroideae

Character	*Putterlickia*	*Gloveria*	*Gymnosporia*	*Moya*
Geographical distribution	mainly eastern parts of S Africa and S Mozambique	Little Karoo and Namaqualand	Africa, Madagascar, S Spain, Arabia, Pakistan, Indomalesia, Phillipines, Australia, Papua New Guinea and the Polynesian islands	Argentina, Bolivia, Paraguay and Uruguay
Habit	shrubs or climbers	shrubs or small trees	suffrutices, shrubs or medium-sized trees	shrubs or small trees
Spines	in axils of leaves or brachyblasts	in axils of leaves or brachyblasts	in axils of leaves or brachyblasts, or terminating brachyblasts	terminating lateral branches
Number of nodes on a spine (modified stems)	one	more than one	usually one	none
Leaf margins	entire, or with few teeth in distal half	entire	entire or with few teeth in distal or both halves	entire or with few teeth
Lamina surface	glabrous	glabrous	glabrous or puberulous	glabrescent or pubescent
Inflorescence	dichasium	dichasium	monochasium or dichasium	fasciculate or solitary
Sexuality of flowers	bisexual	bisexual	mainly unisexual	unisexual
Ovary	3-locular	3-locular	(2)3(4)-locular	2(3)-locular
Locule	6–12- ovulate	3–6-ovulate	2-ovulate	4-ovulate
Capsule surface	smooth and glabrous	smooth and glabrous	smooth, glabrous, rugose, veined or puberulous	smooth, glabrescent or pubescent
Aril colour	orange	pinkish	orange, pinkish, yellow or white	red
Percentage of seed covered by aril	100%	± 100%	± 100%, 60%, 30% or only a rim at the base	± 80%

locule. *Gloveria*, a new monotypic genus of spiny Celastroideae from southern Africa has been described recently (Jordaan & Van Wyk 1998). It is closely allied to *Gymnosporia* from which it is distinguished by always having bisexual flowers and 3–6 ovules per locule. *Gloveria* is similar to *Putterlickia* in having bisexual flowers, but deviates by its fewer ovules per locule, brachyblasts mainly on the spines and more than one node per spine (Table 1).

Gymnosporia is an Old World genus comprising about 80 species and subspecies (Jordaan 1999), occurring in most of Africa, Madagascar and adjacent islands, southern Spain, the near Middle East, Pakistan, India, Sri Lanka, extending to the Far East, Malesia, Papua New Guinea, the Philippines, Taiwan, Queensland (Australia) and Polynesian Islands (Figure 1). Members of *Gymnosporia* are spiny, much-branched, woody, evergreen perennials, varying from dwarf stoloniferous shrublets, to medium-sized shrubs or small trees, usually not taller than 10 m. Plants are mostly dioecious and, therefore, are outbreeders. The flowers are dull in colour (whitish, cream, yellow or rarely red), usually with a disagreeable odour attracting mainly flies. The polymorphic *G. senegalensis* (Lam.) Loes. is the most widely distributed species, ranging from southern Africa northwards to southern Spain and eastwards as far as India.

The nonspiny members of *Maytenus* are distributed mainly in the eastern parts of Africa, Madagascar, Malesia, Australia, and South and Central America. Certain spiny members of Celastroideae (four species) from the arid parts of South America (Argentina and Bolivia) are placed in the genus *Moya* by Grisebach (1874) and Loesener (1942), but in *Maytenus* by Lourteig and O'Donell (1955). In *Moya* there are only two ovules per locule as in *Gymnosporia* and *Maytenus*, but it can be distinguished by the aril which is visible at flowering stage (Loesener 1942), whereas the aril is visible only at the fruiting stage in the other two genera. Other differences between *Moya* and the spiny members of Celastroideae are mentioned in Table 1.

Members of *Gymnosporia* are adapted to both summer and winter rainfall climates, as well as semi-desert regions, but are absent from the Desert Biome (Rutherford & Westfall 1994).

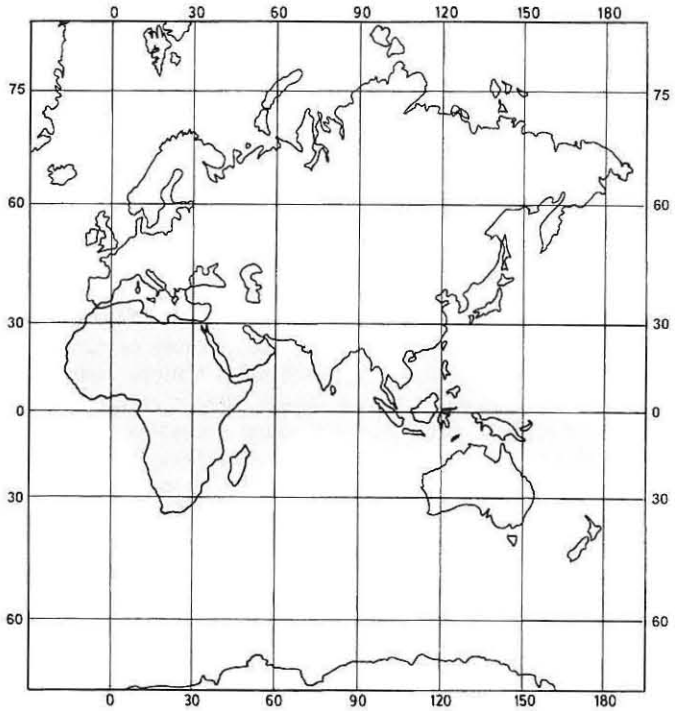

Figure 1 Geographical range of the genus *Gymnosporia*.

Species have been recorded from all three subkingdoms of the Palaeotropical Kingdom (Good 1974) and in all the main phytochoria in Africa (White 1983), but the group is noticeably absent from higher altitudes in the Afromontane Region. Habitats include coastal rocky outcrops and sand dunes, karoo scrub, valley bushveld, open savanna, rocky or grassy hillsides as well as the margins and understorey of afromontane forests. The group is poorly represented in fynbos.

Morley and Toelken (1983), in *Flowering plants in Australia*, separate *Maytenus* and *Gymnosporia* on account of their different inflorescence types and state that *Gymnosporia* is represented by only one species, without mentioning a name, presumably *G. montana* (Roth ex Roem. & Schult.) Benth. Jessup (1984), in a revision of the Celastraceae for the *Flora of Australia*, considers *Gymnosporia montana* a synonym of *Maytenus emarginata* (Willd.) Ding Hou, thus following Ding Hou (1962). *Gymnosporia montana*, the type species of *Gymnosporia*, was described from eastern India. In recent years it has been considered a synonym of *G. senegalensis* by, for example, Sebsebe (1985). The plants occurring in Australia are usually without spines, although brachyblasts are present on older branches. *M. emarginata* has cymose inflorescences, which differentiate it from the other species of *Maytenus s. str.* It is stated by Bentham (1863) that the Australian specimens of *G. montana* are often without spines, as is the case in India as well as in some tropical African specimens of *G. senegalensis*. The leaves of the Australian plants are not coriaceous and glaucous like *G. senegalensis* or *G. emarginata*. Furthermore, the Australian plants have 3-locular ovaries and an aril reduced to the base, whereas *G. senegalensis* has 2-locular ovaries and an aril which partially covers the seed and *G. emarginata* has a 3-locular ovary. This is clearly not the same taxon as *G. senegalensis* nor is it conspecific with the Indian *G. emarginata*. At this stage the material from Malesia, Papua New Guinea, the Philippines, Taiwan, Australia and the Polynesian Islands is best placed under *G. vitiensis* (A.Gray) Seem.

Taxonomy

Amplified genus description

Gymnosporia (*Wight & Arn.*) *Hook. f.* in Bentham & Hooker, Genera plantarum 1: 365 (1862) emend. Loes.: 87 (1942) (*nomen conservandum*). Type species: *G. montana* (Roth ex Roem. & Schult.) Benth.: 400 (1863) (typ. cons.).

Celastrus L. Section *Gymnosporia* Wight & Arn.: 159 (1834).
Gymnosporia Subgenus 1. *Eugymnosporia* Loes. Section 1. *spinosae* Loes.: 207 (1892).
Eucentrus C. Presl: 33 (1844) ex Endl.: 82 (1850).
Polyacanthus C. Presl: 33 (1844).

Small trees, shrubs or rhizomatous suffrutices, usually with spines, rarely without spines, usually with long shoots and weakly or well-developed brachyblasts; plants usually dioecious, monoecious or polygamodioecious, rarely hermaphroditic, glabrous or pubescent. *Branches* terete, angular to striate-angular, lenticels sometimes present; bark smooth or flaking. *Spines* slender to very robust, straight or deflexed, axillary or terminating brachyblasts, occasionally leafy and/or floriferous. *Leaves* alternate or fasciculate on brachyblasts, glabrous or puberulous, subsessile or shortly petiolate, margin entire or with irregular to regular teeth. *Stipules* free, subulate, marcescent. *Inflorescence* cymose, a monochasium, subdichasium or dichasium; cymes few- to many-flowered, solitary or fasciculate in axils of leaves or leaf scars or on spines; peduncles very short or long; pedicels very short or long, articulated at or near base. *Flowers* mostly functionally unisexual with staminodes in female and pistillodes in male flowers, occasionally bisexual, actinomorphic, 5-merous or occasionally 6-merous, hypogynous. *Sepals* unequal or equal, imbricate in bud, margin fimbriate, ciliate or rarely subentire. *Petals* mostly white, cream, yellow, pale green or occasionally pink or red, imbricate in bud, margin ciliate or laciniate, rarely entire, spreading or reflexed. *Disc* intrastaminal, convex or concave, 5–10-lobed, green, yellow or red. *Stamens* attached to base of disc; anthers introrse, with 2 thecae, dehiscing longitudinally. *Gynoecium* syncarpous; ovary with quarter to half immersed in disc, (2)3(4)-locular with 2(3) erect, collateral ovules in each locule; style terete, short or elongate; stigma (2)3(4)-lobed. *Fruit* a dry capsule opening longitudinally, loculicidal and septifragal. *Capsules* variously coloured, globose, obconic-trigonous, triquetrous, pyriform or conic-pyramidal, smooth to rugose, punctate or veined; pericarp semifleshy, chartaceous, coriaceous, woody or ridged. *Seeds* 1–4, glossy, reddish brown or black; aril fleshy or thin, partially to completely covering the seed, or reduced to a rim at base of seed, pinkish, white, yellow, or orange.

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